Foraging ecology of sympatric White-shouldered Ibis *Pseudibis davisoni* and Giant Ibis *Thaumatibis gigantea* in northern Cambodia

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White-shouldered Ibis *Pseudibis davisoni* and Giant Ibis *Thaumatibis gigantea* are two of the most threatened yet poorly known birds of South-East Asia's dry forests. Anecdotal evidence suggests these species have an intriguing combination of ecological similarities and differences, and as they occur sympatrically there may be an opportunity to safeguard them through joint conservation measures. We compared their foraging ecology and proximity to people in an attempt to unravel their ecological differences and better inform conservation. Landscape-scale habitat use was assessed by recording ibis sightings on journeys through a 75,000 ha dry forest landscape; White-shouldered Ibises were surveyed over 526 journeys (totalling 17,032 km) and Giant Ibises over 349 journeys (11,402 km). The ibises showed broadly similar habitat selection, using a range of wetland and terrestrial habitats. Giant Ibises were more often sighted further from settlements than White-shouldered Ibises, with maximum sighting frequency predicted at 9.9 km from villages for the former and 8.3 km for the latter. Giant Ibis may be less tolerant of human disturbance and/or White-shouldered Ibis may be more dependent on traditional land management practices, but the species' differing use of abandoned paddyfield (a habitat typically near settlements) could also be a contributing factor. At waterholes in the dry season foraging Giant Ibis used wetter microhabitats than White-shouldered, suggesting the species occupy different foraging niches. We make preliminary observations regarding Giant Ibis breeding strategy and discuss potential habitat management actions, concluding that, although conservation could address these species simultaneously in dry dipterocarp forest landscapes, their ecological differences must also be taken into account.

INTRODUCTION

Dry dipterocarp forests of South-East Asia contain a distinctive assemblage of species including megafauna such as Asian Elephant *Elephas maximus*, Tiger *Panthera tigris* and Banteng *Bos javanicus*, and large-bodied birds, such as three vulture, four stork and one crane species (Baltzer *et al.* 2001). This biodiversity has suffered various human impacts, namely hunting, habitat loss and degradation, with at least 60 dry forest birds, mammals and reptiles classified as threatened on the IUCN *Red List* in Cambodia alone (Tordoff *et al.* 2005, WCS 2009). While conservation resources are being increasingly directed at this ecosystem, the ecology of the forest and much of its wildlife remains poorly or only partially understood (Songer 2006, CEPF 2007). Of the dry forest birds, two species stand out as amongst the most enigmatic, threatened and poorly studied: the Critically Endangered White-shouldered Ibis *Pseudibis davisoni* and Giant Ibis *Thaumatibis gigantea*.

These two dry forest ibises experienced dramatic declines in the twentieth century (BirdLife International 2001) and, although once widely distributed across South-East Asia, their ranges contracted to become almost entirely confined to Cambodia (BirdLife International 2001). Remaining populations are fragmented and only 250 individual Giant Ibises (BirdLife International 2012b), and 731–856 individual White-shouldered Ibises (Wright *et al.* 2012a) are estimated to remain globally. Conversion of dry forests (for infrastructure, settlement and agriculture, including plantations) and changing local land management are projected to cause further, severe declines in ibis populations (BirdLife International 2012a,b). Conservation action is urgently required to secure these ibises from extinction, but is likely to depend on a scientific understanding of their ecological requirements.

White-shouldered Ibis and Giant Ibis exhibit an intriguing mixture of ecological similarities and differences. The species occur sympatrically in much of their current ranges (historically they occurred together, or in close proximity, in Cambodia and southern Laos: BirdLife International 2001), and while their wet-season foraging ecology remains poorly known (Keo 2008b, BirdLife International 2012a), both forage at seasonal wetlands, known as *trapaengs*, in the dry season (November–May: Keo 2008b, Wright

et al. 2010). Both ibises breed solitarily in canopies of dipterocarp trees and no evidence of migration has been found for either species. Despite these similarities these ibises have contrasting breeding strategies, with White-shouldered Ibis nesting in the mid- to late dry season (December–May: HLW unpubl. data) and Giant Ibis in the wet to early dry season (June–November: Clements *et al.* in press). Available evidence suggests that breeding White-shouldered Ibises forage in exposed substrates at drying-out *trapaengs* (Wright *et al.* 2010). However, why the Giant Ibis breeding season differs so markedly is not yet known, and the habitat use and prey selection of these species have yet to be compared.

The ibises' overlapping ranges and ecology suggest that carefully designed conservation measures could attempt to safeguard both species simultaneously. Conservation that supports local land-management practices may benefit both species, particularly the maintenance of foraging habitat by domestic livestock (Keo 2008b, Wright *et al.* 2010). However, adopting such a strategy requires research into the compatibility of the ibises' ecological requirements and their interaction with people. This study compares White-shouldered Ibis and Giant Ibis foraging ecology, examining habitat selection in the dry forest landscape and microhabitat and prey use at *trapaengs*.

METHODS

Study area

The study was conducted in a c.75,000 ha area within Western Siem Pang and Sekong Important Bird Areas (IBA; centred on 14°17′N 106°27′E), northern Cambodia (Figure 1, Seng *et al.* 2003), an unprotected site with at least 262 individual White-shouldered Ibises and an estimated 80 Giant Ibises (BirdLife International 2012a,b). The area comprises a mosaic of dry dipterocarp forest with patches of grassland (*veals*), river channels, mixed deciduous and semi-evergreen forest, and active and abandoned agricultural land (rice paddy) close to settlements. The climate is strongly monsoonal with average monthly rainfall reaching 333 mm in the wet season and as low as 0.9 mm in the dry season (Thuon & Chambers 2006). Dry forest understorey is burnt annually in the
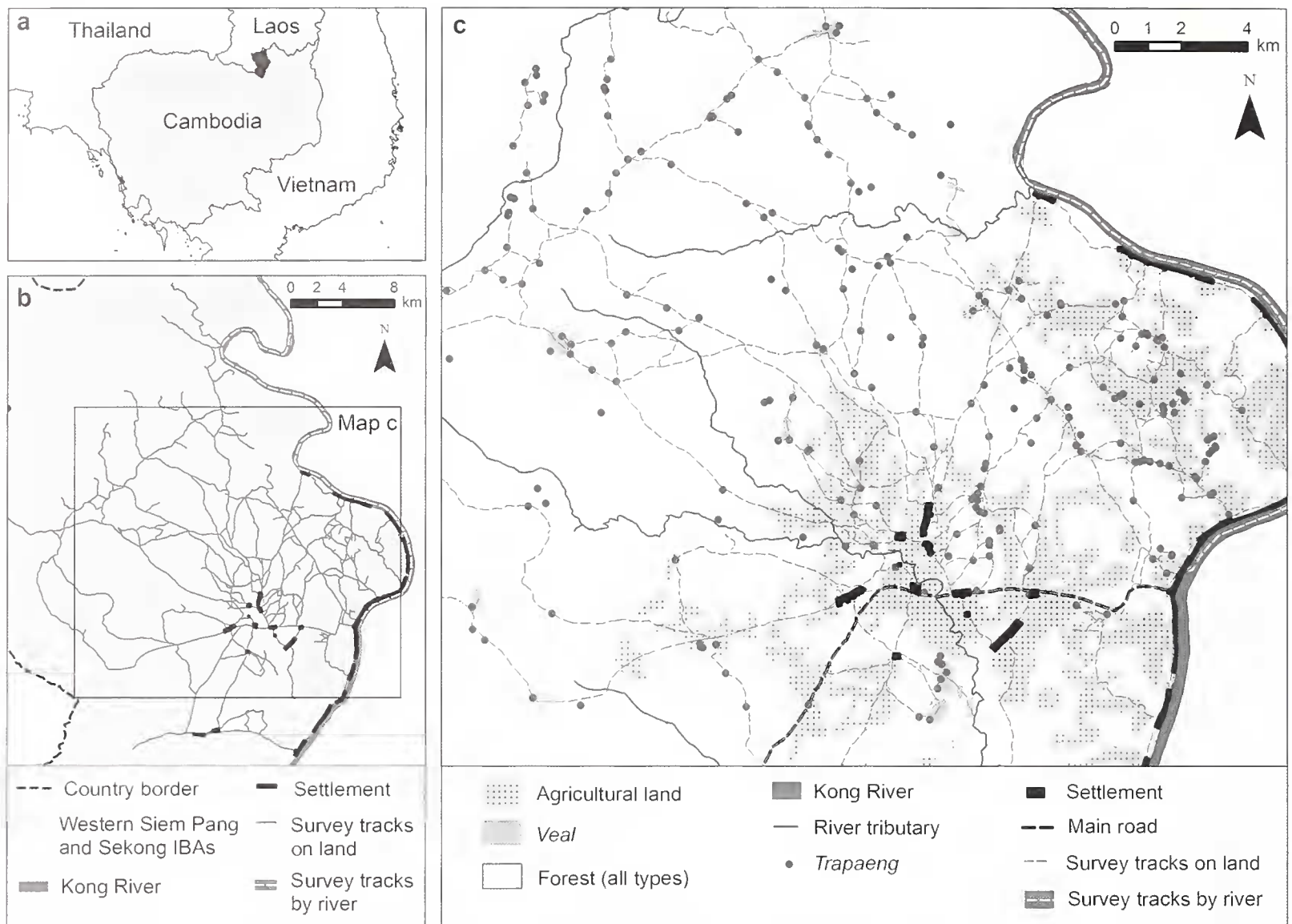
Figure 1. Location of Western Siem Pang and Sekong IBAs in Stung Treng province, Cambodia (a) and extent of survey journeys within the IBAs (b). Map c demonstrates the extent of main habitat types within the core section of the study area. 'Agricultural land' includes cultivated/stubble and abandoned paddyfields.

dry season, largely as a result of anthropogenic fires. *Trapaengs* occur frequently in the landscape and vary in size (0.001–3.4 ha: Wright *et al.* 2010). Water drawdown in *trapaengs* and rivers is dramatic in the dry season, exposing substrates with varied moisture conditions. Villages were concentrated in the south and east of the study area (Figure 1) and inhabited by c.10,000 people (Ministry of Planning 2007).

Surveys of ibis habitat use

Ibis habitat selection was examined at the landscape scale by recording ibis sightings along journeys through the study site. White-shouldered Ibises were recorded during 526 journeys over 22 months between November 2009 and January 2012; the protocol was then expanded also to record Giant Ibises, which were surveyed during 349 journeys over 17 months between March 2010 and January 2012 (a subset of White-shouldered Ibis journeys). Journeys were undertaken systematically as part of travel for wider research and on-site conservation activities, with up to three observers travelling independently per day. Journeys took place along forest tracks and paths, covering 33.9 ± 18.9 km per journey-day (mean ± SD) and were made by motorbike at low speed or occasionally by foot where tracks were inaccessible; 2.4% of journeys were made by boat along main river channels. Journeys were made in both the dry and wet seasons and survey effort (km per journey-day) was similar. Survey routes for each journey were noted on datasheets and recorded using a hand-held GPS.

The survey recorded the location (using a GPS), number, activity and habitat use of ibis with each sighting. Ibises on or taking off from the ground were assumed to be foraging and selected for analysis; other activities (such as loafing or preening) may also take place on the ground but are typically interspersed with foraging bouts and occur in the same habitat (HLW pers. obs.). Habitat was categorised as river channel; *trapaeng*; dry dipterocarp forest; *veal*; cultivated rice paddy; rice paddy stubbles; abandoned paddyfield (unused for more than one season) and mixed deciduous/semi-evergreen forest. The placement of forest tracks was largely independent of vegetation or topographical features, making journeys representative of habitats with the exception of denser semi-evergreen forest (rarely used by either ibis in mainland South-East Asia: BirdLife International 2012a,b), river tributaries and isolated areas of wet-season inundation. Although not traversed, tracks were frequently beside *trapaengs*, allowing them to be surveyed. Much *veal* habitat originated from historic rice cultivation, but swards are typically taller than at more recently abandoned paddies, so these habitats were considered separately; bunds were more apparent in abandoned rice paddies (typically > 10 cm high) than in *veals* (typically < 10 cm or absent), allowing these habitats to be distinguished.

Habitats were mapped with a hand-held GPS during journeys in April 2010. Survey effort per habitat type was quantified in a GIS (ArcMap 9.3, ESRI 2010) by intersecting journey tracks onto the habitat segments they traversed. As tracks went beside *trapaengs*, survey effort for this habitat was quantified by intersecting tracks through buffers surrounding each surveyed *trapaeng*. Buffer size was a factor of *trapaeng* radius and viewable distance (in classes of 0, 20, 40, 60 and 80 m) so that large *trapaengs* visible from far away

accounted for greater survey effort than small *trapaengs* visible only from close by.

The survey protocol was kept simple so that local field staff and villagers (with low technical expertise) could collect consistent data; as distances to observed birds were not recorded, data could not be analysed by a distance-sampling approach. Nonetheless, a preliminary survey did measure the distance from observers to ibises seen on the ground, showing that ibis detectability varied with habitat ($F_{4,34} = 2.71$, $P = 0.046$, distance square-root transformed). Journey distances per habitat segment were therefore multiplied by a habitat-specific estimated transect strip-width, defined by the average sighting distance (or an approximated distance for habitats in which no ibises were observed), to calculate both survey effort and sighting frequency per km². Estimated transect widths may slightly underestimate effective strip-width and therefore overestimate sighting density, but this is unlikely to have caused a directional bias in the findings presented, and population densities were not estimated. Survey areas were aggregated by habitat type and half-month time-periods for analysis.

Foraging observations at *trapaengs*

Ibis microhabitat and prey use were studied at *trapaengs* by observing foraging ibises between December and February in two dry seasons (2008–09 and 2009–10) for seven *trapaeng*-year observation periods: three *trapaengs* in one year and two *trapaengs* in each of the two years. *Trapaengs* were selected to contain a complete gradient of moisture conditions (from pools of water to exposed dry substrate) and maximise the chance of ibis visitation (confirmed by preliminary surveys) to provide foraging data. *Trapaengs* surveyed in both years were observed in different months under novel habitat conditions. Observations were conducted by one observer using a telescope from hides on *trapaeng* perimeters; observations were from dawn until dusk lasting for 3.9 ± 0.7 contiguous days (mean ± SD per site).

Trapaeng microhabitats were defined by four moisture conditions: pools of water, and saturated, moist or dry exposed substrates. Their extents were mapped at each *trapaeng* by sketching homogeneous habitat patches (Wright *et al.* 2010), recording coordinates with a hand-held GPS and measuring dimensions with a laser rangefinder. Maps were georeferenced and digitised in a GIS to calculate patch areas, and area data were aggregated to calculate microhabitat extent as a proportion of each *trapaeng*.

Ibis microhabitat use was measured by instantaneous scan-sampling at six-minute intervals, recording the activity and location (habitat patch) of all ibises present, the latter aided by markers placed around habitat patch boundaries. Prey type and size class (0–2.49 cm, 2.50–4.99 cm and ≥ 5 cm) of each item captured was recorded for ibis individuals during replicate six-minute focal watches. Items of < 1 cm were consumed infrequently and therefore excluded from analysis. Prey biomass was estimated using average ash-free dry mass (AFDM) calculated for a set of prey specimens comprising all prey types and size classes (Piersma *et al.* 1994).

Analysis

Landscape-scale habitat selection was examined by log-ratio analysis (Aebischer *et al.* 1993), comparing proportionate habitat use (from number of sightings) with proportionate habitat availability (from survey effort area) using the half-month period as the unit of replication. Analysis was conducted in Compos Analysis software (Smith 2005) with log-ratios weighted by the square-root of total survey effort area per period. Habitat selection was analysed separately for each ibis species in the dry (White-shouldered Ibis *n* = 23 half-month periods, Giant Ibis *n* = 15) and wet (White-shouldered Ibis *n* = 17, Giant Ibis *n* = 16) seasons. Within the wet season, relative use of *trapaengs* was compared between ibis species with a chi-squared test, contrasting numbers of sightings at *trapaengs*

versus non-*trapaeng* habitats by pooling records from journeys made after March 2010 (when both ibis species were surveyed).

To examine the effect of proximity to people on ibis occurrence, ibis sightings and journey tracks were split using a GIS into five classes of distance to nearest settlement (0–2.49, 2.5–4.99, 5–7.49, 7.5–9.99 and 10–16 km). The effect of distance to settlement (midpoints of the five distance classes, treated as a continuous variable) on ibis sighting frequency (count per distance-to-settlement class per journey-day) was modelled for each ibis species in GLMs with Poisson-distributed error and log link, with log survey effort area included as an offset. Sample units with a journey distance of less than 2 km were excluded to ensure counts were based on adequate survey effort. Non-linear effects of distance to settlement were tested by square-root transformation. Proximity of individual sightings to the nearest settlement (calculated in GIS) was also compared between the two species using a Mann-Whitney test.

The species' microhabitat and prey use at *trapaengs* were statistically compared for the *trapaeng*-year observations in which both ibis species were observed, ensuring comparable survey effort and habitat and prey availability. Species' use of dry *versus* saturated substrate, and of water *versus* other microhabitats combined, were compared using chi-squared tests of the frequency of scan-sampled individuals per microhabitat type. Intake rate (centigrams of AFDM per minute) of two prey groups—(1) amphibians and small invertebrates, and (2) eels and crabs—were calculated using focal watch data and compared between the two species using a Mann-Whitney test.

RESULTS

Ibis sighting frequency and flock size

A total of 446 White-shouldered Ibis and 66 Giant Ibis sightings were obtained from 17,032 km and 11,402 km of survey journeys respectively; 328 White-shouldered Ibis and 51 Giant Ibis sightings were of birds seen on or taking off from the ground and assumed to be foraging ('sightings' refers to foraging birds henceforth). Sighting frequency of foraging White-shouldered Ibis per journey-day was 0.20 ± 0.40 (mean number of sightings per km² ± SD) compared with 0.06 ± 0.31 for Giant Ibis, and mean flock size per sighting was larger (Mann-Whitney test $W_{328,51} = 10,142$, $P = 0.011$) for White-shouldered Ibis (5.9 ± 15.3 birds, mean ± SD) than for Giant Ibis (1.8 ± 0.8 birds). White-shouldered Ibis flock size was greater ($W_{99,229} = 5939$, $P < 0.001$) in the wet (non-breeding) season (10.1 ± 25.1 birds) than in the dry (breeding) season (4.1 ± 7.3); no such difference was found for Giant Ibis.

Landscape-scale habitat selection

White-shouldered Ibis and Giant Ibis both foraged in a variety of habitats within the dry forest landscape, and both showed marked differences in habitat selection between the dry and wet seasons (Figure 2). Both ibises preferred *trapaengs* in the dry season, particularly White-shouldered Ibis which breeds in this season. Giant Ibis also made use of river channels in the dry season, a habitat not used by White-shouldered Ibis in this study. In the wet season, ibises made more equal use of habitats and were found more frequently in terrestrial areas than in the dry season. Both species made use of *trapaengs*, *veals* and dry dipterocarp forest, but White-shouldered Ibises also used abandoned paddyfields (19.4% of wet-season sightings), a habitat in which Giant Ibises were not observed in either season. *Trapaengs* accounted for a greater proportion of Giant Ibis sightings in the wet season than for White-shouldered Ibis (47% and 22% of sightings respectively), and use of *trapaeng* *versus* non-*trapaeng* habitat was greater for Giant Ibis than for White-shouldered Ibis ($x^2_1 = 4.01$, $P = 0.045$). Sighting frequency
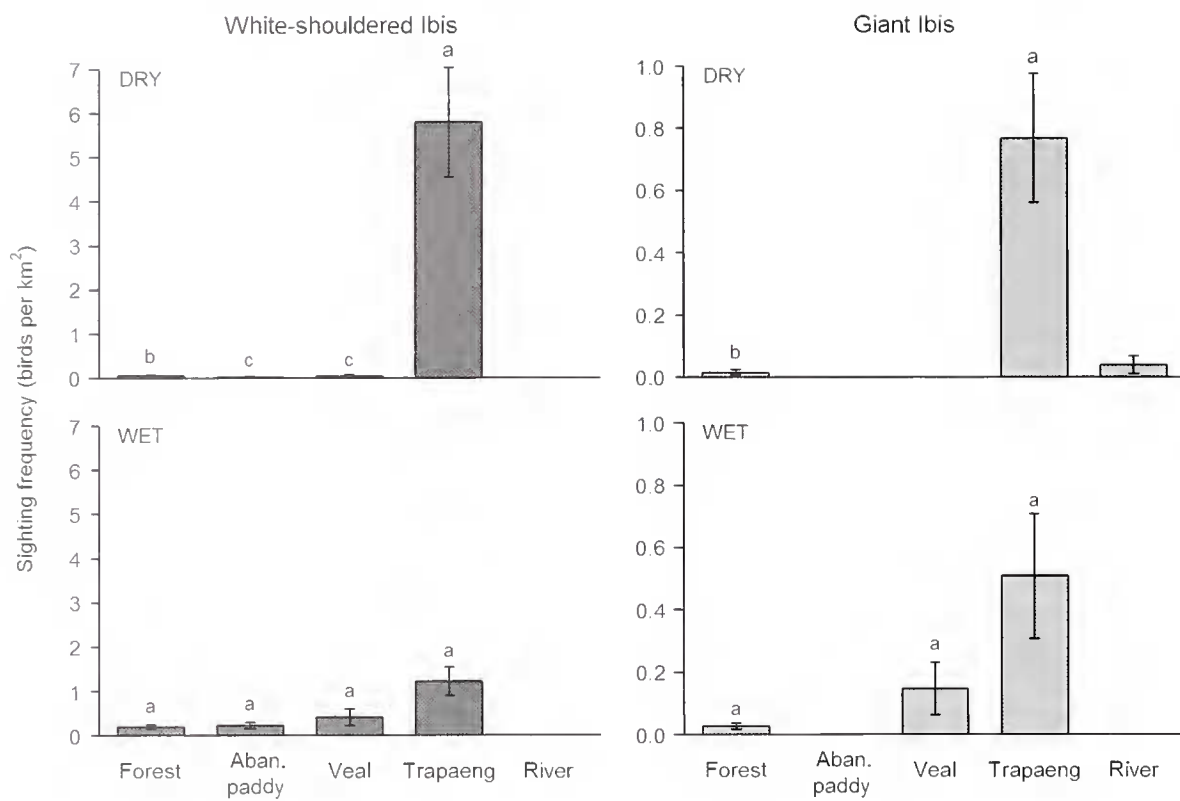
Figure 2. Habitat use of foraging White-shouldered Ibis (dark grey) and Giant Ibis (light grey) in the dry and wet seasons. The dry season corresponds with the White-shouldered Ibis breeding season and Giant Ibis non-breeding season; the wet season is the reverse. All habitats were surveyed in each season; missing bars indicate no birds recorded. Sighting frequency is the average number of foraging ibis sightings per km² per half-month; bars indicate standard error. Ibis habitat use (mean log-ratios of use versus availability) did not differ significantly (P < 0.01) between habitats sharing a common letter; river was surveyed too infrequently to analyse its dry-season selection by Giant Ibis. 'Forest' refers to dry dipterocarp forest, 'Aban. paddy' is abandoned paddyfield.

of White-shouldered Ibis at *trapaengs* in the wet season was also 79% lower than in the dry season, compared with only a 34% difference for Giant Ibis. Three habitats appeared unimportant for foraging ibis: one or fewer sightings were gained (for either species) in rice-paddy stubbles and in cultivated paddy despite the large extent of these habitats in parts of the study area; and fewer than three sightings came from mixed deciduous/semi-evergreen forest, perhaps reflecting this habitat's sparse distribution in the study area and/or poor representation by survey journeys.

## Effect of distance to settlement

Ibis sighting frequency per journey-day was positively related to distance to settlement for both White-shouldered and Giant Ibis (Figure 3), with distance to settlement strongly supported in models for both species; removal of the linear term resulted in Akaike Information Criterion (AIC) increases of > 2 units (63.0 for White-shouldered Ibis and 13.0 for Giant Ibis), while removal of the non-linear term resulted in large AIC increases (96.6 and 22.5 respectively). Predicted White-shouldered Ibis sighting frequency had a steeper response curve with distance to settlement (Figure 3; $n = 1,362$, linear term $\beta = -0.68 \pm 0.17$ 95% CI, non-linear term $\beta = 3.93 \pm 0.79$) than Giant Ibis ($n = 904$, $\beta = -0.85 \pm 0.46$, non-linear term $\beta = 5.41 \pm 2.34$); consequently maximum White-shouldered Ibis sighting frequency was predicted at 8.3 km from settlements compared with 9.9 km for Giant Ibis. Further highlighting this difference, the mean distance to nearest settlement of individual White-shouldered Ibis sightings (5.7 ± 3.3, mean ± SD) was significantly less than for Giant Ibis (7.8 ± 3.4, $W_{323.51} = 5474.5$, $P < 0.001$). White-shouldered Ibis sighting frequency appears to decline after 8.3 km from settlements, but lower sample sizes and overlapping confidence intervals (at 8.3 km versus maximum settlement distance) suggest this result is not robust; using additional classes of 10–12.99 and 13–16 km also did not provide strong evidence for a decline (and resulted in even smaller sample sizes).

Microhabitat and prey use at *trapaengs*

White-shouldered Ibis foraging data were obtained in all seven *trapaeng*-year observations and Giant Ibis data in two, yielding 777 and 117 scan-samples (3,101 and 242 individual bird records) for these species respectively; scan-samples comprised tens of White-shouldered Ibis individuals and a minimum of eight Giant Ibises.

Crude comparison of proportionate microhabitat use shows some apparent similarities between the two ibis species at *trapaengs* in the dry season (Figure 4); both fed in all exposed substrate types and showed proportionally greater use of both dry and saturated substrates than moist substrate. However, relative to other microhabitats, Giant Ibis made greater use of pools of water than White-shouldered Ibis ($x^2_1 = 81.6$, $P < 0.001$) for which only 0.3% of scan-sampled individuals (across all *trapaeng*-years) foraged in

Figure 3. White-shouldered Ibis (dark grey) and Giant Ibis (light grey) sighting frequency (number of foraging ibis sightings per km² per journey-day), averaged by class of distance to settlement (a) and predicted by Poisson GLMs (b): White-shouldered Ibis model AIC = 1585.7, dispersion ratio = 0.77; Giant Ibis model AIC = 376.3, dispersion ratio = 0.31. Bars indicate standard error and dotted lines indicate 95% confidence intervals.
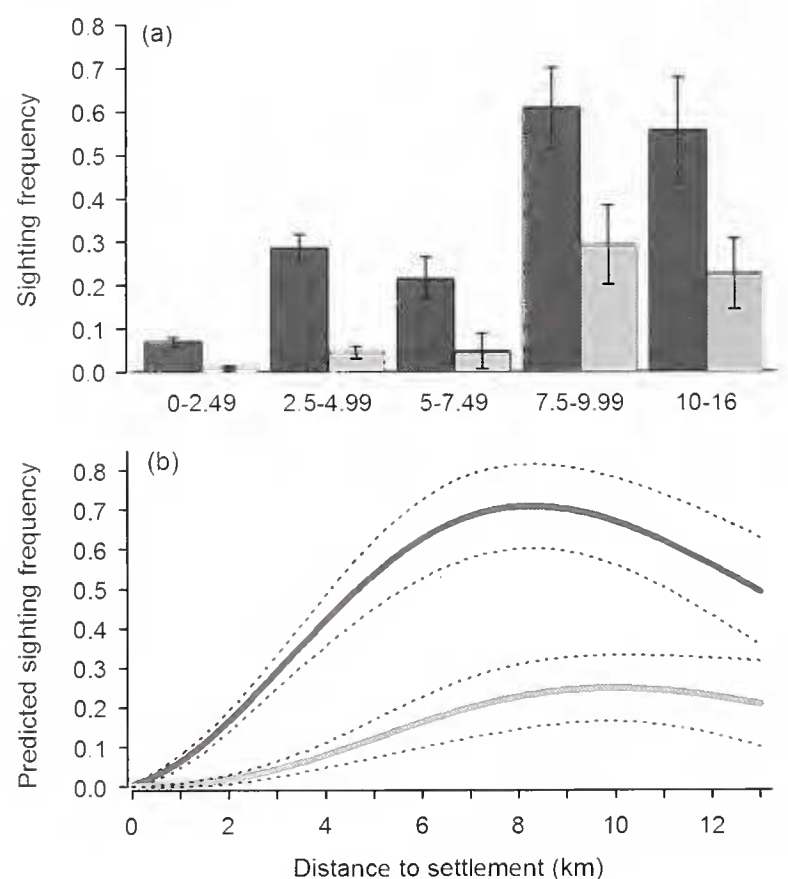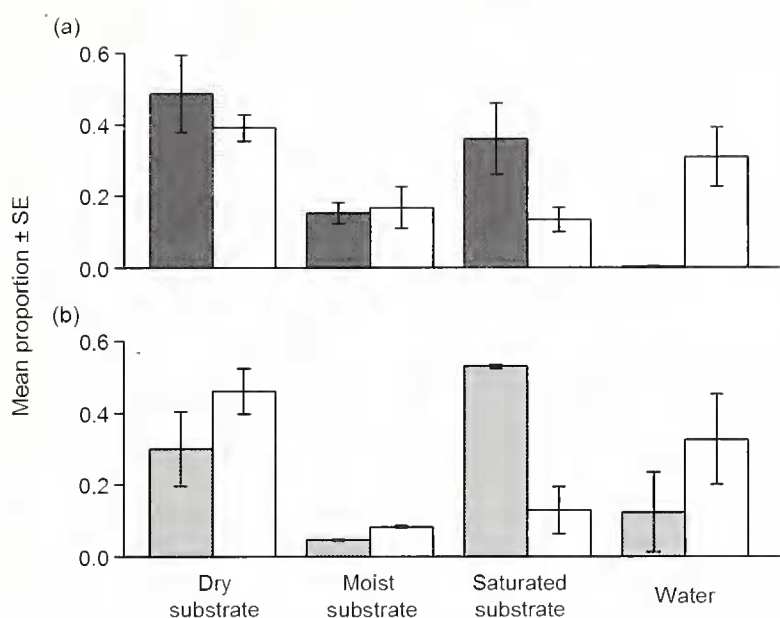
Figure 4. Microhabitat use by (a) White-shouldered Ibis and (b) Giant Ibis at *trapaengs* in the dry season. Proportionate use (grey columns) and proportionate availability (white columns) of moisture conditions were averaged across seven *trapaengs* for White-shouldered Ibis and two *trapaengs* for Giant Ibis. Bars indicate standard error.
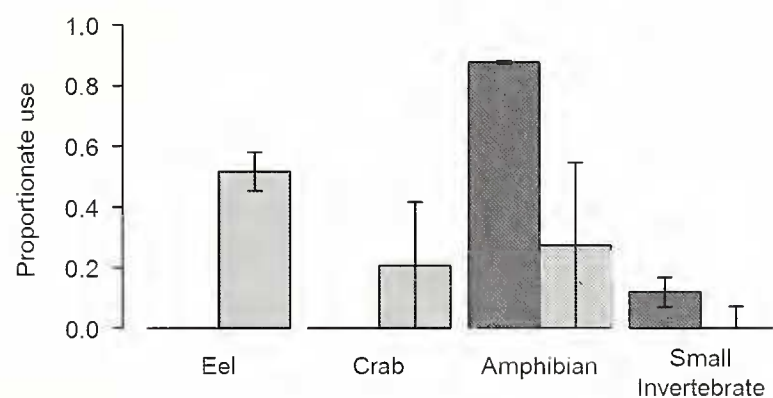

Figure 5. Mean proportionate contribution of prey types to biomass consumed by White-shouldered Ibis (dark grey, at seven *trapaengs*) and Giant Ibis (pale grey, at two *trapaengs*) during foraging bouts. Bars indicate standard error.

water. Furthermore, the ibis differed significantly in their use of saturated *versus* dry substrate ($x^2_1 = 140.7$, $P < 0.001$), with Giant making greater use of the former and White-shouldered greater use of the latter. In terms of proportionate use relative to proportionate availability, White-shouldered Ibis appeared to prefer dry substrate whereas Giant Ibis appeared to avoid it (Figure 4).

Focal sampling at *trapaengs* yielded 89.7 and 3.46 aggregate hours of foraging observation data (from 797 and 40 focal watches) for White-shouldered Ibis and Giant Ibis respectively. Marked differences in diet composition were apparent, with amphibians contributing greatest biomass for White-shouldered Ibis and eels contributing most to Giant Ibis diet (Figure 5). At the two *trapaengs* where both ibis species were observed, combined intake rate of amphibians and small invertebrates was significantly greater for White-shouldered than for Giant Ibis ($W_{349,40} = 3297$, $P < 0.001$). Conversely, combined intake rate of eel and crabs was significantly greater for Giant than for White-shouldered Ibis ($W_{40,349} = 8532$, $P < 0.001$). Prey biomass estimates for a set of ashed prey specimens suggest the average-sized crab caught by either ibis may hold 2.5 times more AFDM than the average-sized amphibian, and the average-sized eel may hold over 5 times more, indicating that Giant Ibis is likely to be consuming considerably greater prey biomass per item caught than White-shouldered Ibis.

DISCUSSION

White-shouldered Ibis and Giant Ibis showed some broad similarities in foraging ecology, including habitat use at the landscape scale. Nevertheless, the relative importance of wetland to terrestrial habitats differed between the species, and contrasting microhabitat and prey use at *trapaengs* suggests these species occupy different foraging niches. Giant Ibises were more often recorded further from settlement than White-shouldered Ibises, suggesting that these species may have different tolerance levels to human disturbance and/or different dependency on traditional land-management practices (assumed to predominate closer to settlements) and habitat types. Conservation could be designed to benefit both ibises simultaneously, but will require careful consideration of their ecological differences.

Landscape-scale habitat selection

White-shouldered Ibis and Giant Ibis used a mixture of dry-forest habitat types, which varied with season. They showed broadly similar habitat use at the landscape scale in contrast to their markedly different breeding strategies. In the dry season, despite rapidly receding water-levels (Wright *et al.* 2010), both ibises preferred to forage in wetland habitats, similar to Sharp-tailed Ibis *Cercibis oxycerca* and Green Ibis *Mesembrinibis cayennensis* habitat selection in the Llanos of Venezuela (Frederick & Bildstein 1992). Mean White-shouldered Ibis sighting frequency was vastly greater at *trapaengs* than in any other habitat in the dry season. This species adopts a foraging strategy well adapted to increasing extents of exposed dry substrates at *trapaengs* in this season (HLW unpubl. data) and access to *trapaengs* may be essential for breeding.

Habitat use in the wet season was more equitable, with both ibis species foraging in a range of wetland and terrestrial habitats. *Trapaengs* continued to be used, although to a lesser degree than in the dry season, and the use of open terrestrial habitats (abandoned paddyfield and/or *veal*) suggests that access to the ground is important, as for most ibis species reliant on terrestrial habitats (del Hoyo *et al.* 1996). Keo (2008b) also noted the value of *veals* as a Giant Ibis foraging habitat, observing a high wet-season abundance of earthworms. White-shouldered Ibis was gregarious in the wet season and large congregations of foraging birds (up to 185 individuals) were observed in *veals* and abandoned paddyfields, indicating the importance of such habitats. Apparent habitat preference and response to settlement proximity may be confounded; abandoned paddyfields were not found more than 4.6 km from settlements, so the absence of Giant Ibis from this habitat may represent avoidance of villages rather than habitat suitability. Conversely, the apparently greater tolerance of White-shouldered Ibis of settlement proximity may reflect its greater use of these habitats rather than a differing response to people *per se*.

Although White-shouldered Ibises were not observed in river channels, rivers appear to constitute important foraging habitat elsewhere in Cambodia and Indonesian Borneo (Sözer & van der Heijden 1997, Timmins 2008). Both species are most likely to forage in river channels with large extents of exposed mud and/or sand (R. J. Timmins *in litt.* 2012); such habitats were rare along surveyed sections of main rivers, and seasonal tributary channels in the wider landscape, perhaps containing the most exposed substrate, were poorly represented by journeys along forest tracks. More dedicated survey of suitable riverine habitat would improve knowledge of its selection by both ibis. Nonetheless, the lack of wet-season sightings along rivers may genuinely reflect prohibitively high water-levels, an effect seen for White-shouldered Ibis along the Mekong River (Timmins 2008).

Proximity to people

Of the two species, Giant Ibis appeared more limited by proximity to people. Foraging birds were observed significantly further from settlement for this species and in models the predicted maximum sighting frequency occurred 1.6 km further from settlements than White-shouldered Ibis. Keo (2008b) found that Giant Ibis typically nested more than 4 km from settlements and preferred to forage at *trapaengs* further from villages, postulating that disturbance and/or persecution may be greater closer to settlements. White-shouldered Ibis appears much more accustomed to people, often roosting and nesting in trees in or around rice paddies—even when in use by people—and is less wary when approached (HLW pers. obs.). Sightings from the early twentieth century, although sparse, also suggest that White-shouldered Ibis was found more frequently in cultivated lands than Giant Ibis (Thewlis & Timmins 1996, BirdLife International 2001). It is possible that White-shouldered Ibis is more opportunistic in its habitat use, while Giant Ibis may make more specialist use of dry-forest landscapes; alternatively, these patterns may reflect an underlying difference in responses to human disturbance. Irrespective of the mechanism, Giant Ibis would appear more vulnerable to human activity and settlement in remote areas, while White-shouldered Ibis's closer proximity to people and less evasive behaviour may make it more vulnerable to hunting, a factor that most probably contributed to its decline, particularly in Laos and Vietnam (BirdLife International 2001). Unchecked habitat conversion, resource extraction, human population growth and settlement expansion, issues requiring urgent conservation action in South-East Asia (CEPF 2007), will threaten both species.

Somewhat contrasting dependencies on traditional land-management practices could also shape these responses to settlement proximity. While both species could benefit from grazing of foraging habitat by livestock (Keo 2008b, Wright *et al.* 2010), White-shouldered Ibis is plausibly more constrained by habitat availability, being a third smaller (in terms of linear body length: del Hoyo *et al.* 1996) and considerably shorter in height than Giant Ibis (HLW pers. obs.). Vegetation growth in *trapaengs*, *veals* and dry dipterocarp forest is substantial in the wet season (HLW unpubl. data) and may reach more than double White-shouldered Ibis body height (Wright *et al.* 2010), potentially restricting this species's use of habitats otherwise still accessible to Giant Ibis. More frequent White-shouldered Ibis sightings in areas closer to settlements could reflect a stronger requirement for grazed habitat and bare ground, where livestock densities are highest (Wright *et al.* 2010). The possible decrease in White-shouldered Ibis sighting frequency beyond 8.3 km from settlements would further support this. The effect of people and livestock on ibis abundance deserves further study to understand the potential trade-off between the negative effects of human disturbance (particularly for Giant Ibis) and the positive effects of land-use practices. Examining ibis distribution in a study landscape with a steeper gradient of livestock density and greater maximum distance to settlement than occurred in this study area would help in clarifying this potential effect.

Foraging ecology at *trapaengs*

The dry-season foraging ecology of White-shouldered Ibis and Giant Ibis has been examined elsewhere (Keo 2008a, Wright *et al.* 2010, Wright in press). Having observed only a small number of Giant Ibis feeding at two *trapaengs*, this study cannot draw major new conclusions on this species's foraging strategy and we limit the discussion to a preliminary comparison of the two species. Similarities included both species' use of all exposed substrate types, and shared use of the amphibian resource at *trapaengs*. Although Keo's (2008b) study (from January to April) found amphibians contributed a major part of Giant Ibis diet (as is the case for White-

shouldered Ibis), this study found them to be of only marginal importance. However, our survey took place earlier in the dry season when wetter conditions may have sustained more of the aquatic prey seemingly favoured by this species. The most notable differences in microhabitat use were the avoidance of water and apparent selection of dry substrate by White-shouldered Ibis, contrasting with Giant Ibis's greater use of water and saturated substrates. Prey use reflected this with the contribution of aquatic prey to Giant Ibis diet (83% of consumed biomass) far exceeding that in White-shouldered Ibis diet (0.4%). Average biomass of prey items consumed by Giant Ibis was 263% greater than of items consumed by White-shouldered Ibis, perhaps explaining the large disparity in body size between these species, or demonstrating the Giant Ibis's need to consume sizeable prey to sustain its large body size.

Despite some similarities in foraging ecology, the contrasting use of wet microhabitats suggests the ibises may occupy different foraging niches at *trapaengs*, at least in the early to middle dry season. Studies of ibis incidence at *trapaengs* add further evidence, with Giant Ibis selecting *trapaengs* with greater extent of wet mud (Keo 2008b), but White-shouldered Ibis showing no such selection (Wright *et al.* 2010). The ibises' morphology may also point to a degree of niche separation: the White-shouldered Ibis's neck is feathered from the body to the top of its hindcrown, whereas Giant Ibis has feathering along only one-third of its neck-length. The latter may be an adaptation for a bird that more regularly submerges its head and upper neck in water or wet mud, although the presence of bare skin may also aid thermoregulation (Buchholz 1996, Ward *et al.* 2008). When in shallow water, Giant Ibis forage by probing with bill slightly agape (Eames 2011, HLW pers. obs.), matching the technique used by other ibis (e.g. Kushlan 1979) but not witnessed for White-shouldered Ibis.

Giant Ibis breeding strategy

The wet-season foraging ecology of these ibises is still very poorly known (Keo 2008b, BirdLife International 2012a); examining the ibises' relative foraging success for wet season prey types and habitats will inform conservation and shed light on the Giant Ibis's breeding strategy. Accessing tall and densely vegetated wet-season habitats may be easier for Giant Ibis (given its larger body size) than for White-shouldered, allowing it to reach the prey-rich earthworm mounds found in dry dipterocarp forest and particularly *veals*. A longer, thicker bill may also be more effective at probing for earthworms. Terrestrial habitats, particularly *veals*, can become inundated in the wet season and *trapaeng* water-levels increase substantially (HLW unpubl. data). Greater use of *trapaengs* in the wet season, a greater tendency to forage in wet microhabitats, and longer legs and bill all indicate that Giant Ibis may be better adapted to foraging in flooded conditions. Giant Ibis may therefore have a broader range of suitable wet-season habitats in which to forage and provision chicks.

Implications for habitat management

White-shouldered Ibis and Giant Ibis both used a mosaic of habitat types, requiring protection and management of habitats at the landscape scale. *Trapaengs* are important breeding-season habitats for both species, but a range of terrestrial habitats must also be available, particularly in the wet season. Broadly similar habitat use indicates that conserving a suite of dry forest habitats will benefit these sympatric ibis species simultaneously. The use of open habitats such as *veals* and abandoned paddyfields suggests these features should be protected and kept open; the latter deserve particular attention as they occur in close proximity to settlement and may be particularly vulnerable to agricultural and urban expansion. Clearings could be created to improve habitat availability in landscapes dominated by dense dry forest, and managed (e.g. by livestock grazing) to ensure they remain accessible. Knowledge of

the ibises' wet-season foraging ecology would be valuable to assist the design and management of these open areas.

Maintaining the extensive rearing of domestic livestock is likely to be important to both ibis species—a requirement shared with many other threatened species in pastoral and mixed farming systems (Wright *et al.* 2012b). Domestic livestock keep sward heights low at *trapaengs*, *veals* and in dry dipterocarp forest, maintaining habitat suitability for White-shouldered Ibis (HLW unpubl. data). Domestic buffalo are key grazers at *trapaengs* and may also be useful in creating areas of saturated substrate to benefit Giant Ibis at *trapaengs* (Keo 2008b). Both ibises will be affected if a reduction in livestock causes long-term ecological succession and *trapaeng* sedimentation. Further study should investigate whether introducing buffalo or cattle in landscapes where both domestic livestock and wild herbivores are lacking can improve habitat suitability for these species, and whether animal wallowing may contribute to *trapaeng* creation. Annual dry-season fires are another component of traditional dry forest land-management, resulting in reduced sward heights; this could be a benefit to ibises foraging in terrestrial habitats and also deserves further research.

While conservation could benefit White-shouldered and Giant Ibises simultaneously, care should be taken to ensure that interventions do not overlook their ecological differences. In particular, safeguarding Giant Ibis is likely to require that large areas of undisturbed habitat are protected from development and human interference, contrasting with the White-shouldered Ibis's potentially stronger need for habitat management. Human disturbance and hunting risk require close attention in interventions that expand, enhance or maintain traditional management practices. Equally, maintaining dry-season water-levels at *trapaengs* for the benefit of Giant Ibis or other wildlife (Keo 2008b) should not be undertaken to the extent that the exposed substrates (including dry ground) preferred by breeding White-shouldered Ibis become scarce or unavailable.

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